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The New World filarial genus *Molinema* Freitas & Lent, 1939 (Nematoda: Onchocercidae), with a description of four new species parasitic in the Echimyidae (Rodentia)

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Abstract

Four new species of *Molinema* (Filarioidea: Onchocercidae), parasites of echimyid rodents in South America, are described: *M. algardneri* n. sp. from *Proechimys amphichoricus, M. barbarae* n. sp. from *P. cayennensis*, both in Venezuela (Rio Negro and Cerro La Neblina, respectively), *M. peruviensis* n. sp. from *P. steerei* in Peru (lower Urubamba), and *M. nattereri* n. sp. (= *Filaria diacantha* Molin, 1858 pro parte) from *Echimys ? didelphoides* (= *Loncheres rufa*) in Brazil (Matto Grosso). They differ from each other and from the previously described species in the following characters: flat or concave head, cephalic ratio (distance between cephalic papillae in median view/lateral view), size and shape of the buccal capsule, length of the oesophagus, cuticular ornamentation of the female body, length of the ovijector, thick or slim female tail, *area rugosa*, long or short filament in the left spicule, heel in the right spicule, respective position of postcloacal papilla pairs 5 and 6, shape of the caudal lappets, terminal point present or absent, and the microfilariae. *Molinema*, which belongs to the worldwide *Dipetalonema* line, is distributed in two of the ten families of the Caviomorpha (South American Hystrichognathi have extended their distribution in South America since the early Oligocene). Nine species are parasitic in the Echimyidae (suborder Caviida); they have a short oesophagus and a complete or reduced set of precloacal papillae (four or three pairs). Two species are parasitic in the Erethizontidae (Erethizontida) and might be more primitive in having a well-developed oesophagus. However, the type-species *M. diacantha*, of which a female specimen was studied, has a large buccal capsule and has evolved concave head, while *M. arbuta* has a reduced buccal capsule and primitive flat head. This last species is a parasite of a Nearctic porcupine and probably represents a small line of *Molinema* which migrated to the north with its hosts when communications were established between the two American continents 3 mya (Pleistocene). *M. sprenti*, the unique parasite of the Castoridae in North America, is considered to be derived from this group by capture.

Introduction

During surveys of wild mammals in the Amazonas region of Venezuela and Peru, filarial nematodes inhabiting the body-cavity were recovered. They belonged to either *Litomosoides* Chandler, 1931 or *Molinema* Freitas & Lent, 1939, two New World genera of the subfamily Onchocercinae. This paper concerns *Molinema*, which is a member of the *Dipetalonema* line (Chabaud & Bain, 1976), characterised mainly by "a right spicule in form of a complex, cone-shaped structure" and the head laterally elongated, "flat or concave" (Anderson & Bain, 1976).

This study initially comprises an analysis of the type-species, *M. diacantha* (Molin, 1858), a female worm from a coendu kept in the MNHN collection, followed by a description of the material collected. This comprised three new species, each recovered from a different species of the echimyid genus *Proechimys* Allen. In contrast to this narrow speci-

ficity, Molin reported the type-species in two families, the Erethizontidae, to which belongs the type-host, and the Echimyidae. It was also possible to examine this material, which is preserved in the Collection of Evertebrata- Varia at the Naturhistorisches Museum Wien (NMW). The specimens, which are young adult filariae, making comparative analysis difficult, represent a fourth new species.

Finally, an attempt is made to present a plausible hypothesis for the evolution of the genus *Molinema*, based on morphological data, host range and geographical distribution.

Materials and methods

The parasites were collected from the abdominal and thoracic cavities of freshly killed hosts, preserved in ethanol (70%) and cleared in lactophenol for morphological study. Microfilariae were described after being dissected from the uteri. All measurements are in micrometres, unless otherwise specified; those of the holotype or allotype are presented first, followed by the range of the paratypes and other studied examples in parentheses; for the microfilariae, the mean is given first, followed by the range in parentheses. The buccal capsule is defined by its height (from its junction with the oesophagus to the mouth) and its width (maximal external diameter of the capsule). The cephalic ratio is the distance between the cephalic papillae in median view divided by this distance in lateral view. The tail ratio is the tail length divided by its width at the anus. The male caudal pairs of papillae are numbered according to Chabaud & Petter (1961): precloacal pairs 1 to 4; postcloacal pairs 5 (internal pair) and 6 (external pair); the last pairs 7 to 10 are too reduced to be numbered. When specimens were in sufficient number, spicules were dissected out.

Types are deposited in the Laboratorio de Helmintología del Museo de Historia Natural, Universidade Nacional Mayor de San Marcos, Lima (MUSM), Colección de Parasitología, Museo de Biología, Universidade Central de Venezuela (CPMBUCV) and United States National Parasite Collection, USDA (USNPC), and other specimens in Helminthological Collection, Muséum National d'Histoire Naturelle, Paris (MNHN).

Vegetation types are classified according to UNESCO (1981). Host names are those of Wilson & Reeder (1993), with the original names in parentheses. A problem concerned the identification of the echimyid host of Molin's material. According to this author and the document attached to the material conserved in the NMW, the host was *Loncheres rufa*, a male trapped in October, in the Matto Grosso. We were unable to find the host name even in the papers of Wagner (1845, 1847) and Pelzeln (1883) in which is reported the whole of Natterer's collection of mammals; it was probably a field identification by Natterer. However, an examination of these papers discloses a male rodent, collected in November, 1826 in the same region, which, in our opinion, is very probably the original host: *Loncheres armata*, renamed recently *Echimys didelphoides* Desmarest by Emmons (1993), subfamily Echimyinae (= Loncherinae).

Results

Two characters of the males, which are not usually studied, appear common to all species examined: the *area rugosa*, which is present not only anterior to the cloaca but on the tail; and the apex of the testis, which is placed just posterior to the level of the oesophageal-intestinal junction. The lamina of the left spicule is composed of a proximal longitudinally folded part and a narrow distal part (filament) which may or may not be equal in length. In the female, glandular cells attached to the vagina, close to the vulva, were often noticed; the unpaired ovijector may present a specialised musculature when it is very long. Deirids are always present, but reduced. The caudal extremity in either sex bears two lateral lappets and a terminal point or tubercle, and is similar to that of the infective larva (Bain & Chabaud, 1986), or the terminal point has regressed. Microfilariae are unsheathed and have an attenuated anterior end with a small hook and a posterior end tapering to a fine non-nucleated point.

Molinema diacantha (Molin, 1858) (Figure 1)

Host: *Sphiggurus villosus* (Cuvier) (*Coendou villosus*) (Erethizontidae).
Locality: East of Rio de Janeiro, Brazil.
Material: One female worm collected by Travassos in 1924 and identified by Lent and Freitas in 1938 (No. 687 TW, MNHN collection, given by the Instituto Oswaldo Cruz in 1976).

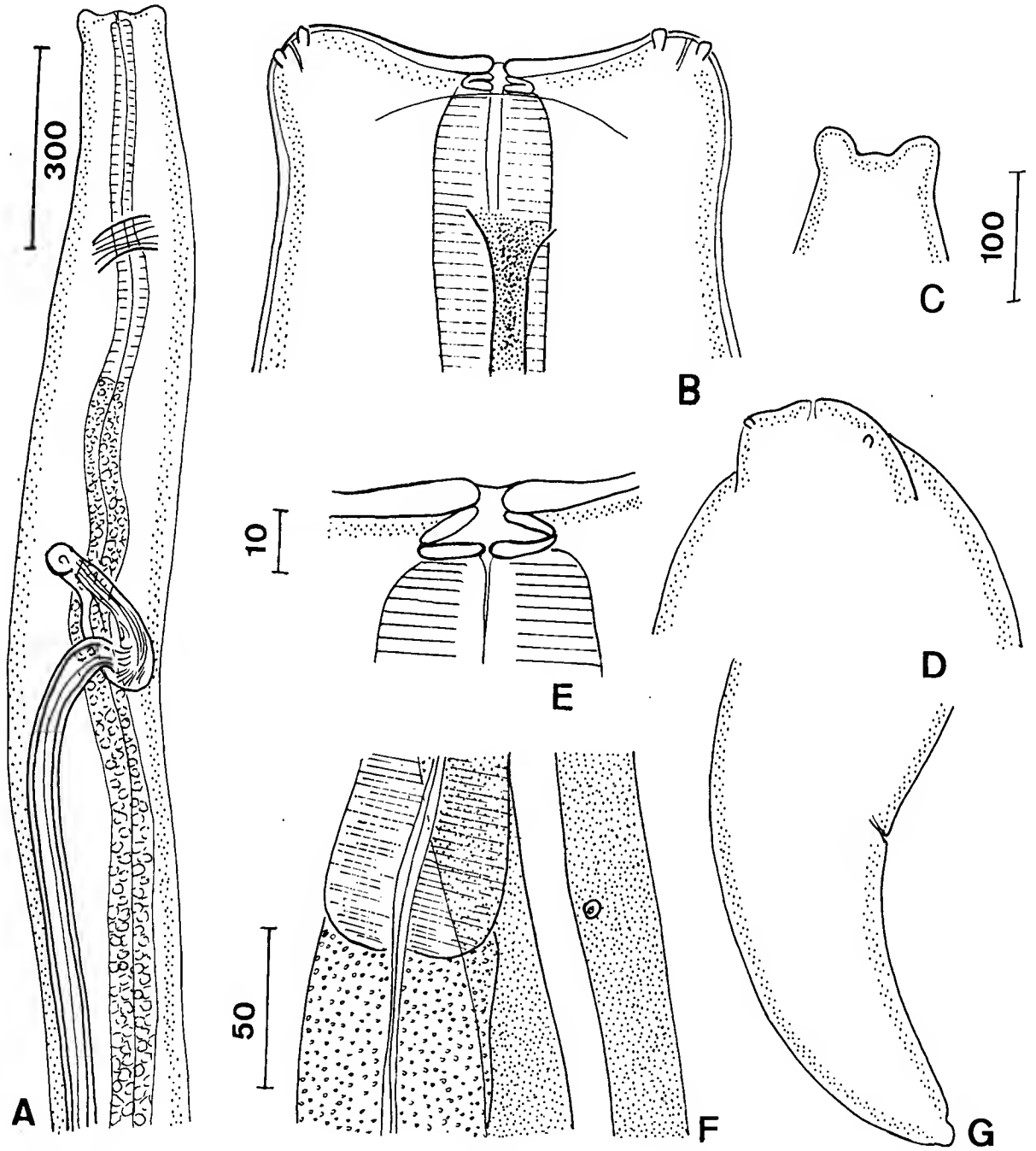

Figure 1. Molinema diacantha, female. A. Anterior region, ventral view; B. Head, ventral view (the ventral chord is shown); C. *Idem*, showing the exaggerated head concavity in the transiently deformed worm; D. *Idem*, lateral view; E. Buccal capsule; F. Deirid and oesophagus at level of the abrupt change into the glandular region (lateral chord is shown); G. Tail, lateral view. *Scale-bars*: A, 300 μm; B,D,F, 50 μm; C,G, 100 μm; E, 10 μm.

Description

Female (one specimen). Length 78.7 mm. Maximum width 330 at mid- body. Head concave in median view (its shape is easily distorted when the worm is rolled over for examination under the cover-slip and becomes very concave). Bulging of lateral edges of head accentuated. Distance between cephalic papillae 128 in median view, 37 in lateral view; cephalic ratio 3.46. Buccal capsule 10 high, 21 wide. Oesophagus 4,895; muscular and glandular parts of equal diameter at their junction but with abrupt change of structure. Deirids at this level, 532 from apex. Vulva 825 from apex. Tail 268 long, conical and bent ventrally, with 2 rounded terminal lappets; tail ratio 2.3.

Comments

Molin (1858) erected the taxon *Filaria diacantha* for material collected by Natterer from *Coendou prehensilis* (Linnaeus) (= *Hystrix prehensilis*) in the Matto Grosso (Caiçara), Brazil. The detailed description of the species was given by Freitas & Lent (1939) using filariae recovered from *Sphiggurus villosus* (Cuvier) (*Coendou villosus*) in the eastern part of Rio de Janeiro. Material from the same host species was used in the later descriptions (Anderson, 1955; Freitas, 1964) and in the present study. It is not certain that the two groups of material are identical, but this question cannot be resolved, because Molin's type-material, in the Museum of Vienna, now consists only of an unusable small fragment of a female worm.

The specimen examined showed that, in normal conditions, the head is much less concave than previously illustrated (Anderson, 1955), the buccal capsule is middle-sized, the diameter of the glandular oesophagus may equal that of the muscular part (our specimen) but the change in internal structure is abrupt, and deirids are present.

***Molinema algardneri* n. sp.** (Figures 2,3)

Type-host: *Proechimys amphichoricus* Moojen (Echimyidae).
Site: Body-cavity.
Type-locality: Isla Sarama, Rio Negro, Amazonas, Venezuela. (01°54′16″N, 67°06′27″W), 50 m, tropical humid forest or tropical ombrophilous lowland forest.
Prevalence: 4 / 4.
Type-material: Holotype male CP-MBUCV No. 4351; allotype female CP- MBUCV No. 4352; paratypes: 3 males and 2 females CP-MBUCV No. 0385 (host number 162-010384).
Other studied material: 2 males and 2 females MNHN No. 37HS (host number 161-010384). *Etymology*: Named for Alfred L. Gardner, who collected and identified the hosts, in recognition of his contributions to Neotropical mammalogy.

Description

General. Head flat or slightly depressed. Rectangular cephalic shield expanded laterally, constricted in sagittal plane, wider and with rounded edges laterally. Oral opening minute and round. Buccal capsule wider than long, triangular in dorso-ventral view, composed of 2 thin segments; anterior longer. Oesophagus with muscular and glandular parts of similar diameter. Deirids slightly asymmetrical and without salient point.

Male (holotype and 4 specimens). Length 45.4 (43.2-49.3) mm. Maximum width 222 (210-219) at mid-body, width at nerve-ring 97 (88-96), at oesophago-intestinal junction 145 (122-157). Distance between cephalic papillae in median view 46 (48-58), in lateral view 27 (24-32); cephalic ratio 2.1 (1.7-2.2). Buccal capsule 4 (4-7) high and 14 (12-18) wide. Oesophagus 1,266 (1,127-1,224); muscular portion 351 (351-460) and glandular portion 915 (667-852) long. Nerve-ring 228 (204-240) and deirids, in one paratype, 214 and 268 from apex. Tail 336 (261-324) long, slightly attenuated, with short terminal tubercle; width at cloaca 75 (61-84); tail ratio 4.48 (3.67-5.31); lappets conical, terminating in narrow to digitiform protuberance, 15 (14-15) long by 10 (9-10) wide. Phasmids at base of lappets. Single unpaired precloacal papilla and 4 pairs of precloacal papillae; fourth often paracloacal; postcloacal pairs 5 and 6 almost in transverse line; pair 6 larger; one papilla, left or right, in posterior third of tail. *Area rugosa* 2,300 long; transverse ridges 2-3 high; distance between ridges 10. Left spicule 287 (270-278) long; handle 121 (130-140) long; lamina 165 (135-148) long, terminating in long membranous filament. Right spicule 151 (159-184) long, proximally thick; distal part cone-shaped with heel. Spicule-ratio 1.70 (1.52-1.90).

Female (allotype and 4 specimens). Length 87.3 (89.1-96.1) mm. Maximum width 278 (324-336) at mid-body, 114 (114-132) at nerve-ring, 126 (132-151) at vulva, 162 (162-181) at oesophago-intestinal junction. Body cuticle with infrequent tiny bosses. Distance be-

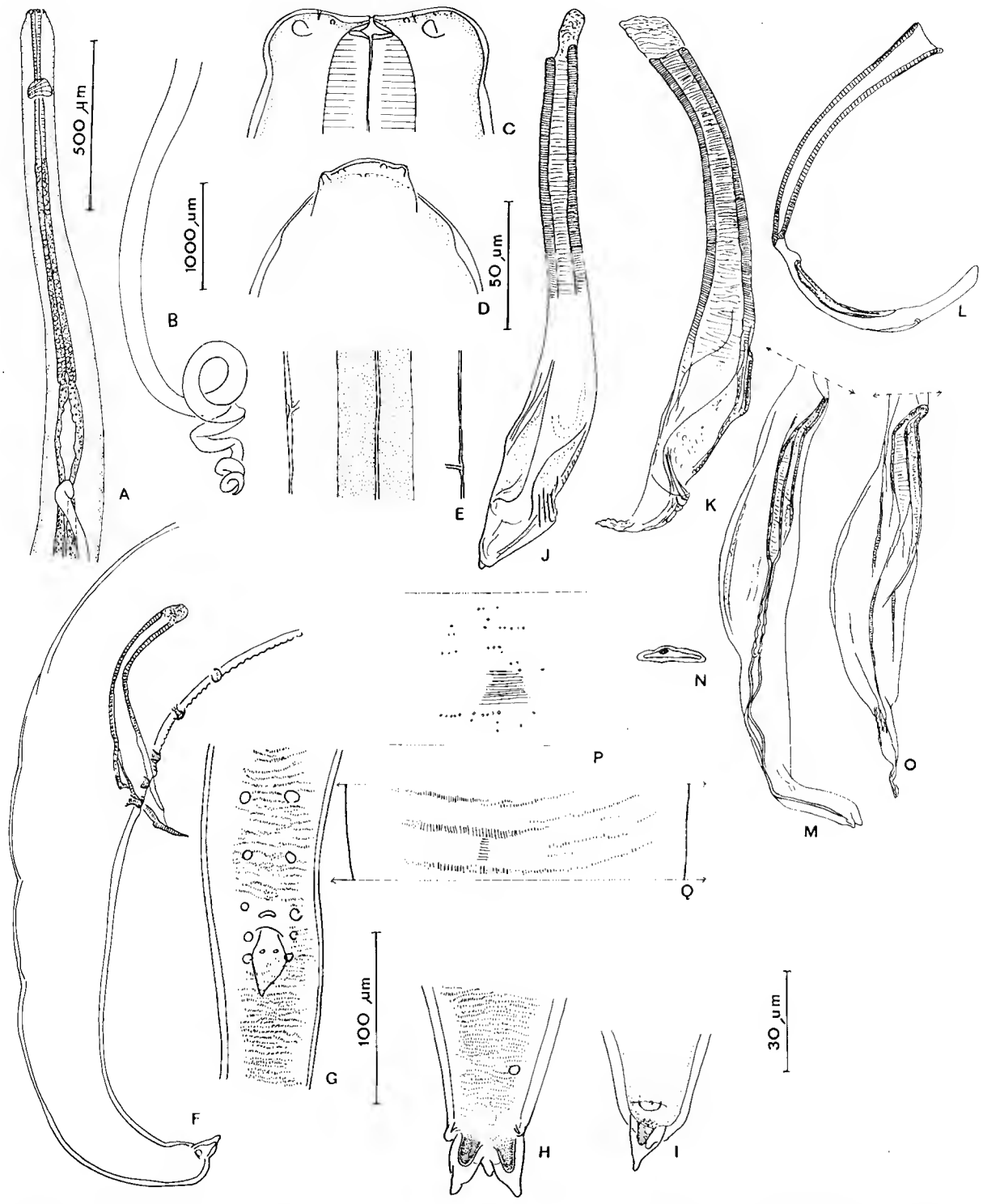

Figure 2. Molinema algardneri n. sp., male: A. Anterior region; B. Posterior region; C. Head, ventral view; D. *Idem*, lateral view; E. Deirids, ventral view; F. Tail, lateral view; G.*Idem*, ventral view; H. Caudal extremity, ventral view; I. *Idem*, lateral view; J. Right spicule, ventral view; K. *Idem*, lateral view; L. Left spicule, lateral view; M. Blade of dissected left spicule, lateral view; N. *Idem*, optical transverse section; O. Blade of dissected left spicule of *M. dessetae*, lateral view; P. Anterior end of *area rugosa*; Q. *Area rugosa*, at mid-length. *Scale-bars*: A, 500 μm; B, 1000 μm: C,D, 50 μm; E,F,G, L, 100 μm; others, 30 μm.

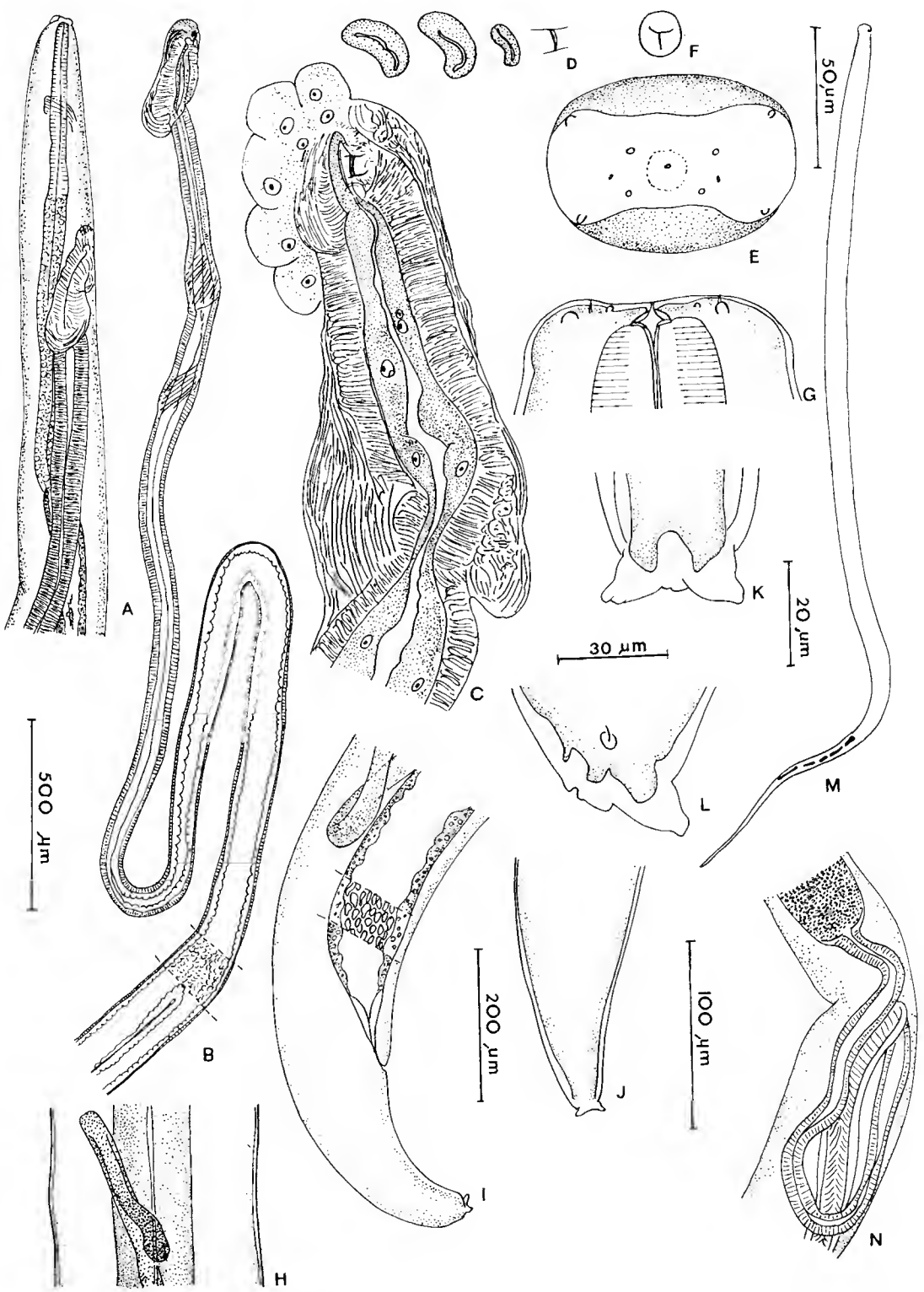

Figure 3. Molinema algardneri n. sp., female: A. Anterior region, lateral view; B. Ovijector; C. Vagina with glandular cells, ventral view; D. Optical sections of initial part of *vagina vera* from vulva (on right) to the distal part (on left); E. Head, apical view; F. Optical section of anterior part of oesophagus; G. Head, ventral view; H. Apex of ovary (lateral chord is shown); I. Posterior region, lateral view (detail of cellular structure of the intestine is shown); J. *Idem*, ventral view; K. Caudal extremity, ventral view; L. *Idem*, lateral view; M. Microfilaria; N. Oviduct and uterus with spermatozoa. *Scale-bars*: A,B,N, 500 µm; C,D, 100 µm; E,F,G, 50 µm; H,I,J, 200 µm; K,L, 30 µm; M, 20 µm.

tween cephalic papillae in median view 52 (51 and 61), in lateral view 27 (27-30); cephalic ratio 2.3 (1.9-2.6). Buccal capsule 7 (7-8) high and 14.4 (14-16) wide. Oesophagus 1,074 (1,086-1,224); muscular portion 390 (378-432) and glandular portion 684 (708-792). Nerve-ring 310 (240-394) from anterior end. Vulva oesophageal, 591 (618-666) from apex; vagina 273 (276-285) long with large granulated cells attached anteriorly; unpaired ovijector 4,000 and 5,500 long, with specialised musculature of oblique fibres 500 and 750 from vagina. Tail robust, conical, 252 (210-282) long, truncated at tip; width at anus 114 (120); tail ratio 2.21 (1.75-2.35). Lappets divergent, broad at base, terminating in narrow protuberance, 19 (15-21) long by 15 wide. No terminal tubercle. Phasmids ventro-lateral and anterior to caudal lappets.

Microfilaria (6 specimens): length 175.2 (165-185); width 4.3 (4.0- 4.5).

Comments

In addition to *M. diacantha*, seven species are described in the genus *Molinema*: *M. bifida* (Molin, 1858) from *Kannabateomys amblyonyx* (Wagner) (= *Dactylomis amblionix* (sic)) at Ipanema, Rio de Janeiro, Brazil and redescribed by Freitas and Lent (1939), Anderson (1955) and Freitas (1964); *M. travassosi* (Artigas & Pacheco, 1933) from *Myocastor coipus* (Molina) in Brazil, probably near Sao Paulo; *M. arbuta* (Highby, 1943) described from *Erethizon dorsatum* (Linnaeus) in northern Minnesota, USA; *M. sprenti* (Anderson, 1953) from *Castor canadensis* Kuho in Ontario, Canada; *M. dessetae* (Bain,1973) described from *Proechimys oris* Thomas (identified as *P. guyannensis* (E. Geoffroy) in Bain, 1973) in Parà State, Brazil; *M. proechimyis* (Esslinger,1974) described from *P. trinitatis* (J. A. Allen & Chapman) [= *P. guyannensis* (E. Geoffroy)] collected in Trinidad; and *M. raposoensis* (Esslinger,1974) described from *P. semispinosus* (Tomes) in Valle, Colombia. All are different from our specimens.

M. arbuta and *M. sprenti* have a flat head like these specimens but are distinguished by three main characters: the small buccal capsule (3 and 4 high in the females, respectively, after the figures of Highby, 1943 and Anderson, 1953); an oesophagus twice the length (means of 2,200 to 2,400 in males and females); and the long microfilariae (280-297 and 322-430 respectively, vs 165-180). In addition *M. arbuta* has a small cephalic ratio (1.4 *vs* 1.9-2.6), postcloacal papillae in tandem compared to an almost transverse line, and a short right spicule (112-125 vs 159-184); *M. sprenti* has a left spicule with the handle longer than the blade, and in the female the tail is long and spirally coiled (390-690 *vs* 210-280).

M. diacantha is distinguished by the very long oesophagus (4,200- 4,700 and 4,560-5,980 respectively in male and female), the concave head and the greater cephalic ratio (3.4 *vs* 1.9-2.6 in the females); it also has a slightly larger buccal capsule (10 × 21 *vs* 7-8 × 14-16 in the female), a much shorter ovijector (1,660-2,240) and the left spicule has a blade shorter than the handle and a short filament.

M. bifida and *M. proechimyis* are distinguished by the concave head, the longer buccal capsule (14-21 and 18, respectively), the rather long female body (respectively 135-161 and 167 on average), and the three pairs of precloacal papillae. In addition, *M. bifida* has a small cephalic ratio (1.6), a short right spicule (120-130) and a short left spicule (200-220) with a short filament, no terminal caudal tubercle in both sexes and, according to the original description, a microfilaria 660-700 long and 4 wide. *M. proechimyis* has a rectangular cephalic shield which is not enlarged and rounded laterally, and a thick rounded tail in the female (tail ratio 1.1-1.9 vs 1.8-2.4), with parallel lappets (versus divergent).

M. travassosi is also distinct because of its concave head (Artigas & Pacheco, 1933), and very great body length (260 mm) and width (560-620); in males, the fourth pair of papillae is anterior to the cloaca (compared to paracloacal); in the female a terminal caudal tubercle is present; and the microfilariae are sligthly longer (189-200).

The two last species, *M. raposoensis* and *M. dessetae*, have, like our specimens, a flat head and medium-sized buccal capsule and oesophagus. However, *M. raposoensis* has a cephalic shield which is very elongated laterally (cephalic ratio 3) and rectangular in shape, three pairs of precloacal papillae, a right spicule without a heel, a female tail which is cylindrical, slender and usually three times longer than wide, a short left spicule (182- 237) with a short filament, no subterminal papilla, no terminal caudal tubercle in either sex, and microfilariae which are 193-249 long. *M. dessetae* has a rectangular cephalic shield, postcloacal papillae pairs 5 and 6 in tandem, a left spicule with a short filament (Figure 1,O) and microfilariae 210-289 long.

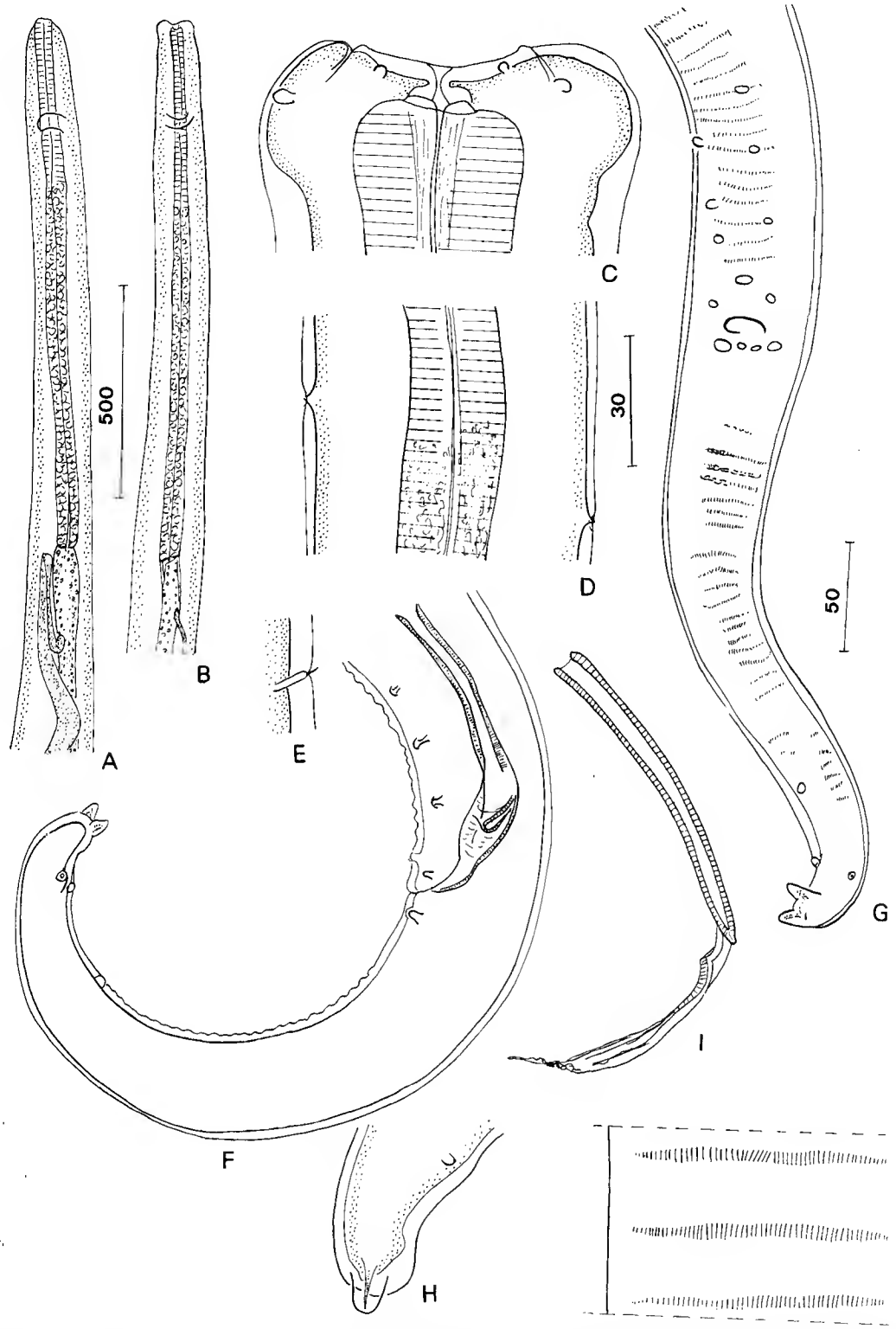

Figure 4. Molinema barbarae n. sp., male: A. Anterior region holotype; B. *Idem*, another example; C. Head, ventral view; D. Deirids, at level of the beginning of glandular oesophagus, median view; E. *Idem* (detail); F. Tail, left lateral view; G. *Idem*, ventral view; H. Caudal extremity, lateral view; I. Left spicule, lateral view; J. *Area rugosa* at mid-length. *Scale-bars*: A,B, 500 μm; C,E,J, 30 μm; others, 50 μm.

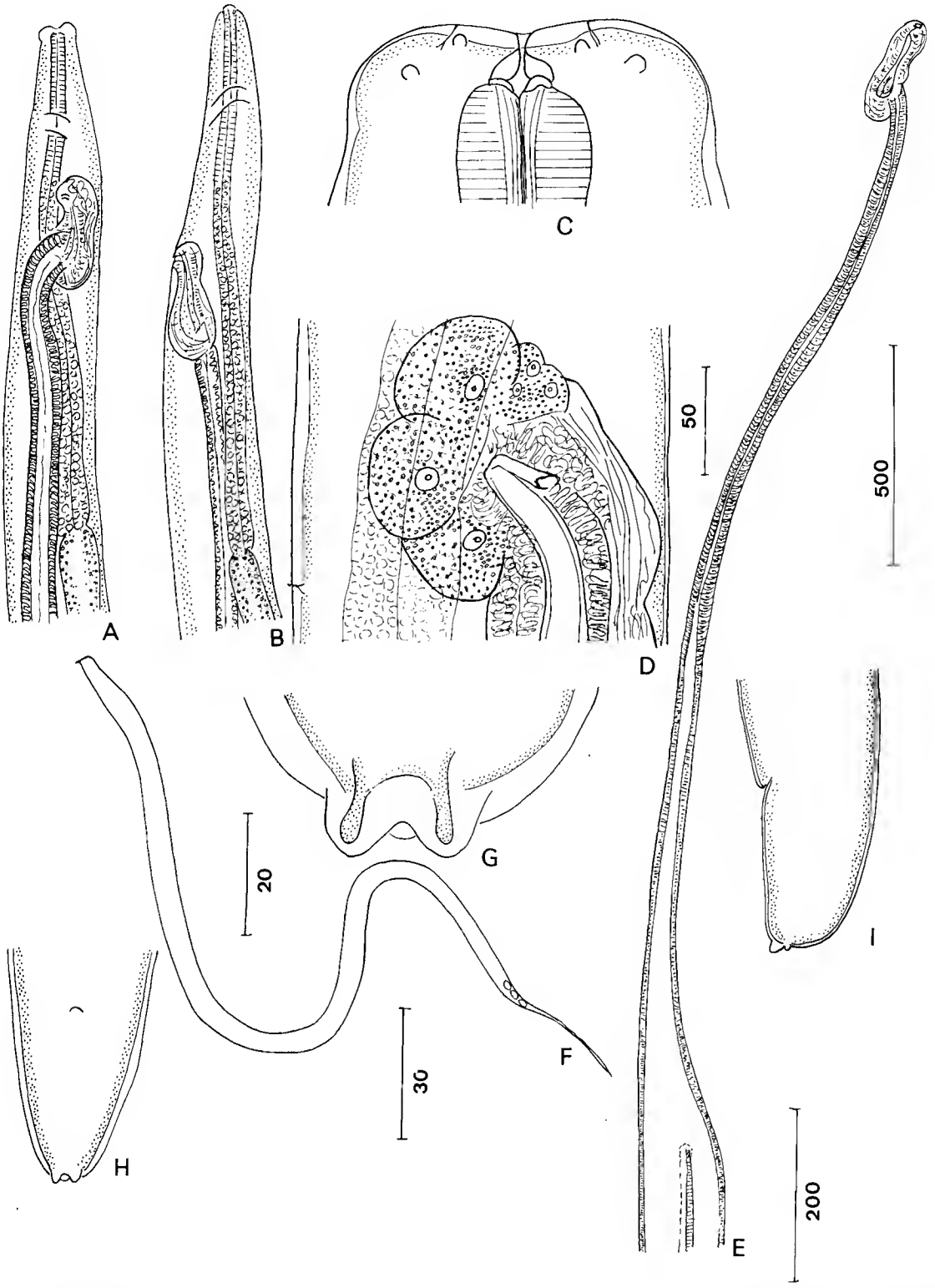

Figure 5. Molinema barbarae n. sp., female: A. Anterior region, ventral view; B. Anterior region, lateral view; C. Head, ventral view; D. Deirids, vulva and anterior part of vagina with glandular cells; E. Ovijector; F. Microfilaria; G. Caudal extremity, lateral view; H. Tail, ventral view; I. *Idem*, lateral view. *Scale-bars*: A,B,E, 500 μm; C,G, 30 μm; D, 50 μm; F, 20 μm; H,I 200 μm.

***Molinema barbarae* n. sp.** (Figures 4, 5)

Type-host: *Proechimys cayennensis* (Desmarest) (Echimyidae)
Site: Body-cavity.
Type-locality: Base Camp, Cerro La Neblina, Amazonas, Venezuela (00°49′50″N, 66°09′40″W), 140m, tropical humid forest or evergreen ombrophilous forest.
Prevalence: 3 / 5.
Type-material: Holotype male CP-MBUCV No. 0387; allotype female CP- MBUCV No. 4353 (host number 18-200384).
Other studied material: From one host, two anterior parts of males, respectively CP-MBUCV No. 0388 and MNHN No. 188 HS (host number 19-200384); from another host, one female MNHN No. 187 HS (host number 36-200384).
Etymology: Named for Barbara Szymanska, the senior author's wife, who collected these and many other parasites.

Description

General. Head slightly concave. Buccal capsule with thick walls. Oesophagus divided; muscular and glandular parts of similar diameter. Tail without terminal tubercle in either sex.

Male (holotype and 2 anterior portions). Length 44.8 mm. Maximum width 241 (164-201) at mid-body; width at nerve-ring 121 (75-101), at oesophago-intestinal junction 153 (120-173). Distance of cephalic papillae in median view 58 (60-60), in lateral view 29 (30-32); cephalic ratio 1.9 (1.9-2.0). Buccal capsule 9.6 (9-10) high and 16.3 (16-17) wide. Oesophagus 1,236 (1,242-1,296) long by 44 wide; muscular portion 396 (384-401) and glandular portion 842 (840-912). Nerve-ring 246 (195-225) and deirids, with short point, 432 from apex. Tail 349 long; width at cloaca 62; tail ratio 5.63; lappets conical, 12 long and 9 wide. Unpaired precloacal papilla 18 from cloacal opening; 4 precloacal pairs; postcloacal papillae 5 and 6 in transverse line; pair 6 larger; 3 asymmetrical ventro-lateral papillae in posterior third of tail and single ventral papilla 85 from tail tip. *Area rugosa* on tail and anterior to cloaca, 6,500 long; transverse ridges 3.5-4.0 high; distance between ridges 17-18. Left spicule 295 long; handle 160 long; lamina 135 long with short filament. Right spicule 160 long, with heel. Spicule-ratio 1.84.

Female (allotype and one specimen). Length 111.9 and 104.4 mm. Maximum width 318 and 342 at mid-body; width 123 and 128 at nerve- ring, 181 and 197 at vulva, and 228 and 241 at oesophago-intestinal junction. No tiny cuticular bosses on body. Distance between cephalic papillae in median view 48 and 45, in lateral view 30 and 26; cephalic ratio 1.67-1.7. Buccal capsule 11 and 8 high and 14 and 16 wide. Oesophagus 1,251 and 1,164 long by 45 wide; muscular portion 429 and 381; glandular portion 822 and 783. Nerve-ring 193 and 224, and single deirid with small point 450, from anterior end. Vulva oesophageal, 587 and 462 from the anterior end; vagina 246 long and 256 wide; unpaired ovijector 2,800 and 2,500 long. Tail 200 and 206 long; width at anus 162 and 132; tail ratio 1.23 and 1.56. Lappets conical, parallel, 21 long by 15 wide.

Microfilaria (4 specimens): length 172 (168-172), width 4 (3.8-4.0).

Comments

Two species, *M. dessetae* and *M. algardneri*, are close to these specimens according to the four pairs of precloacal papillae, the size of the buccal capsule and oesophagus, the body length and the thick tail in the female. However, they differ in several characters. *M. dessetae* has the pairs 5 and 6 of the papillae in tandem, an *area rugosa* with ridges which are short and less widely spaced (1.5 and 6 respectively vs 3.5-4 and 17-18), a long tail in the female (390 *vs* 200-206) but short in the male (255 *vs* 349), a long ovijector (5,200) and long microfilariae (210-289). *M. algardneri* has a conical tail in the female which is bent at its mid-length, and the tail ratio is 1.75-2.35 compared to cylindrical and a straight tail with a ratio of 1.23-1.56, a long ovijector (4,000-5,500) with specialised musculature, a short *area rugosa* with ridges which are short and less widely spaced (2,300, 2-3 and 10, respectively), a left spicule with a long filament, and a tail with terminal tubercle in the male. In addition, both these species have a tail with divergent lappets in the female.

***Molinema peruviensis* n. sp.** (Figures 6,7)

Type-host: *Proechimys steerei* Goldman (Echimyidae).

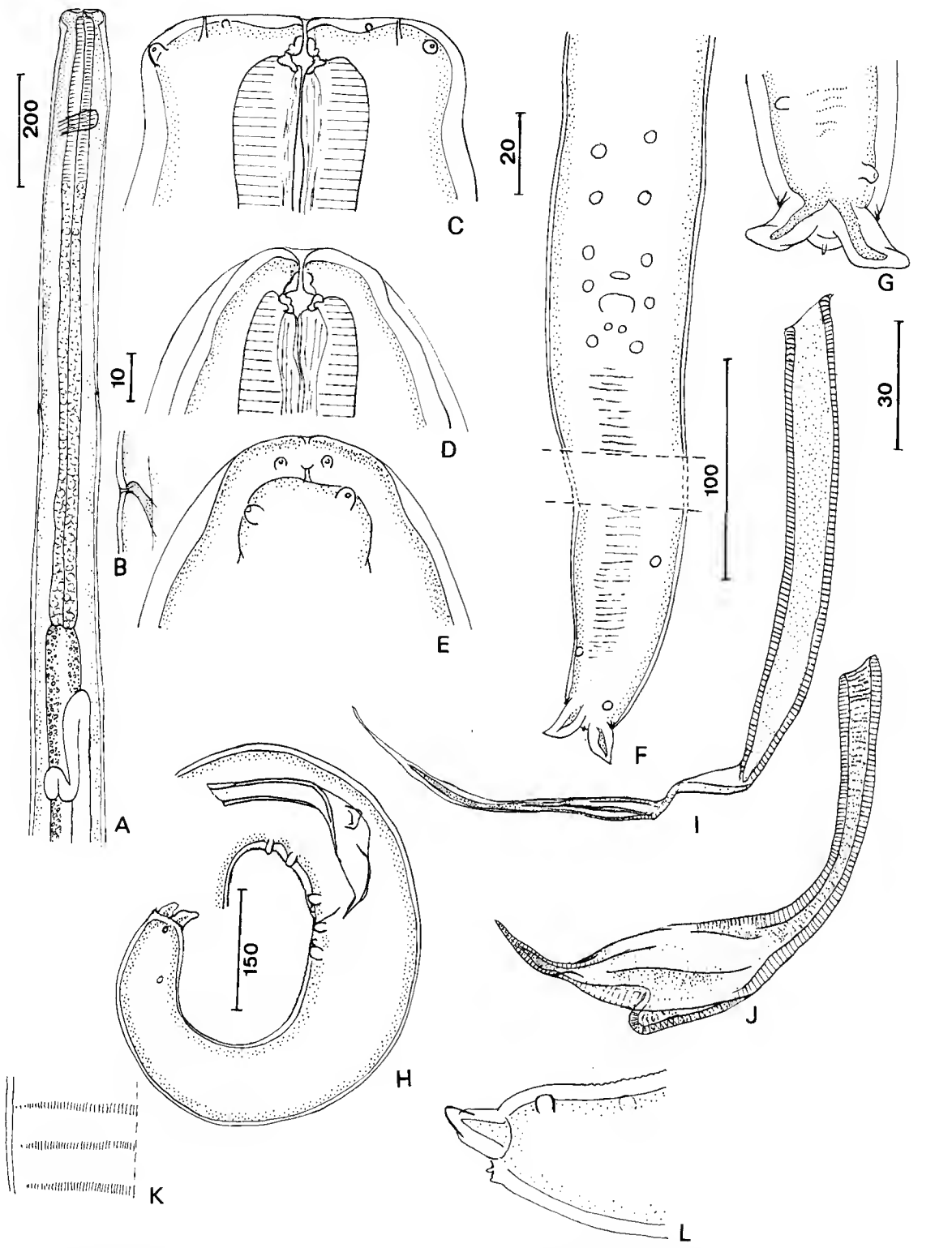

Figure 6. Molinema peruviensis n. sp., male holotype: A. Anterior region median view (deirids at mid-length of glandular oesophagus); B. Deirids, detail; C. Head, ventral view; D. Buccal capsule, lateral view; E. Head, lateral view; F. Posterior region, ventral view (only the cloacal region and extremity are shown); G. Caudal extremity, ventral view; H. Tail, left lateral view; I. Left spicule, lateral view; J. Right spicule, lateral view; K. *Area rugosa*, at mid-length; L. Caudal extremity, left lateral view. *Scale- bars*: A, 200 μm; B, 10 μm; F, 100 μm; H, 150 μm; I,J,L, 30 μm; others, 20 μm.

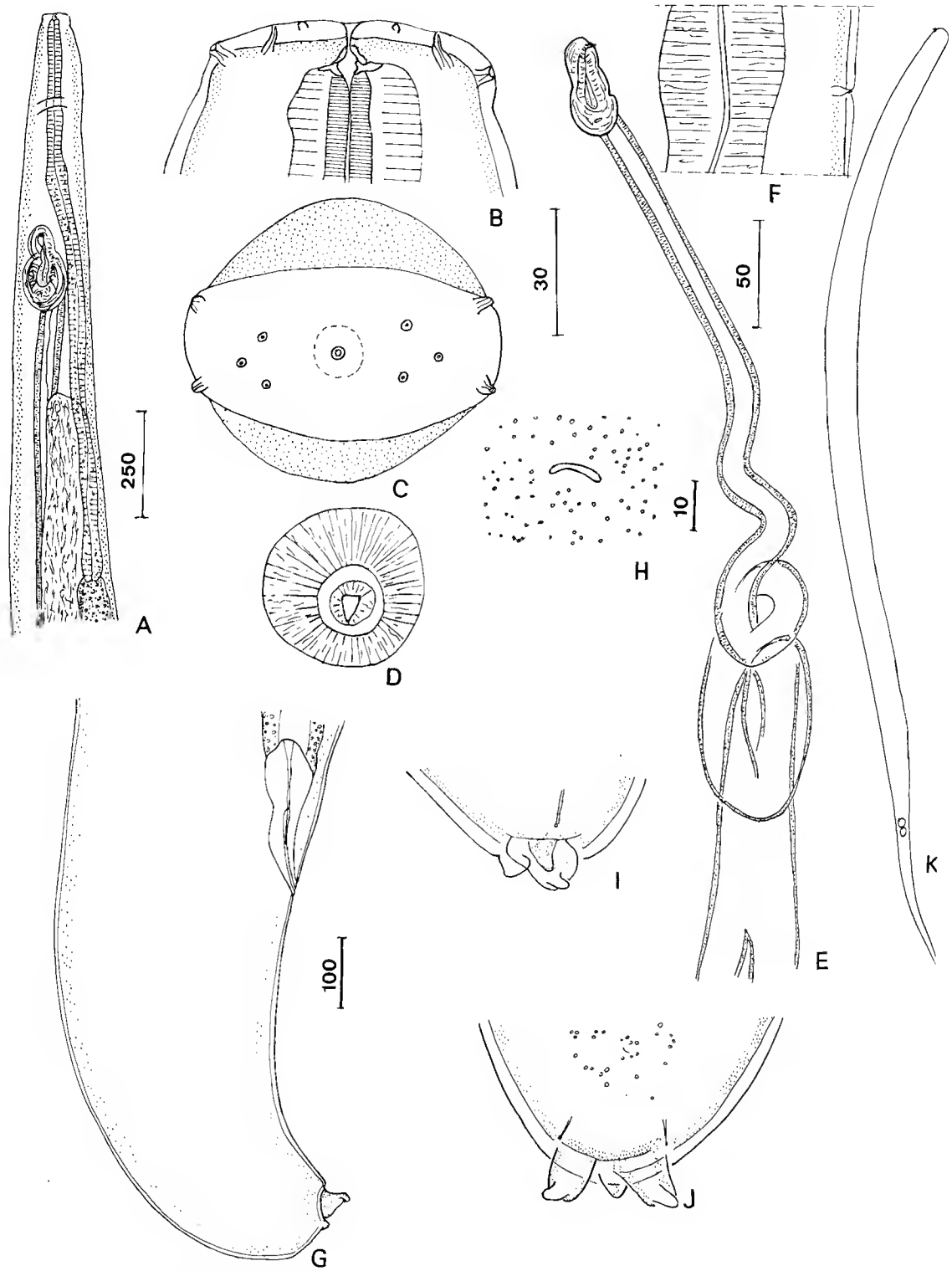

Figure 7. Molinema peruviensis n. sp., female: A. Anterior region, ventral view; B. Head, ventral view; C. *Idem*, apical view; D. *Idem*; optical section of buccal capsule (circular lumen) and oesophagus (triangular lumen); E. Ovijector; F. Deirid, lateral view; G. Tail, lateral view; H. Anal region with cuticular ornamentation, ventral view; I. Caudal exremity, lateral view; J. *Idem*, ventral view; K. Microfilaria. *Scale-bars*: A,E, 250 μm; B,C,D,I,J, 30 μm; F, 50 μm; G, 100 μm; H,K, 10 μm.

Site: Body-cavity.
Type-locality: San Martin 3 well site, close to the Cashiriari River, lower Urubamba region, Cusco, Peru (11°45′S, 72°44′W), 400 m., tropical humid forest or tropical evergreen seasonal lowland forest.
Prevalence: 2/2. Ten *Proechimys simonsi* Thomas trapped at the same place were negative.
Type-material: Holotype male and allotype female in the Helminthological collection of MUSM; paratypes: 2 females in USNPC and 2 females in MNHN No. 189 HS (host number 76-010597).
Other studied material: One female in MUSM and one female CP-MBUCV No. 4354 (host number 22-010597).

Description

General. Head flat. Cephalic shield rectangular and well expanded laterally. Buccal capsule as long as wide. Oesophagus divided; muscular and glandular parts of similar diameter. Tail with terminal tubercle in either sex, but tiny in male.

Male (holotype). Length 46.8 mm. Maximum width 192 at mid-body; width at nerve-ring 108, at oesophago-intestinal junction 120. Distance between cephalic papillae in median view 70, in lateral view 26; cephalic ratio 2.5. Buccal capsule 12 high and 12 wide. Oesophagus 1,068 long by 42 wide; muscular portion 294. Nerve-ring and deirids without point 228 and 691, respectively, from anterior end. Tail 292 long, 66 wide at cloaca; tail ratio 4.42; terminal tubercle truncated and with point; lappets 24 long by 8 wide. *Area rugosa* 4,500 long; ridges 2-3 high, spaced 10-14. One median precloacal papilla; 4 pairs of precloacal papillae arranged in 2 groups of 2 pairs each; postcloacal pair 5 slightly anterior to pair 6; pair 6 larger; 3 asymmetrical ventro-lateral papillae on posterior third of tail. Left spicule 214 long; handle 126 long and lamina 88 long with short filament. Right spicule 154 long, with well-developed heel; spicule-ratio 1.39.

Female (allotype and 6 specimens). Length 84.4 (81.0-96.5) mm long. Maximum width 260 (252-300) at mid-body; width at nerve-ring 140 (102- 126), at vulva 150 (121-150), at oesophago-intestinal junction 198 (174- 216). Tiny cuticular bosses in posterior region, with higher density anterior to anus and on tail. Distance between cephalic papillae in median view 64 (59-66), in lateral view 26 (24-33); cephalic ratio 2.5 (2.0-2.7). Buccal capsule 12 (14-16) high and 15 (12-17) wide. Oesophagus 1,320 (1,140- 1,458) long by 50 wide; muscular portion 381 (301-435) and glandular portion 939 (795-1,130). Nerve-ring 210 (195-234) and one deirid 550 from anterior end. Vulva oesophageal, 510 (525-642) from anterior end; vagina 200 (195-372) long; ovijector 3,500 long, widening far from uterine division. Tail 230 (171-243) long; width at anus 109 (100-140); tail ratio 2.1 (1.64-2.40). Lappets divergent, broad at base, terminating in short protuberance directed laterally, 23 (17- 23) long by 17 (15-17) wide.

Microfilaria (10 specimens): length 199 (179-230), width 5.6 (6.0- 5.1).

Comments

These specimens have a relatively large buccal capsule, like *M. bifida* and *M. proechimyis*, but these two species are distinguished by the concave head, the long body of the female, and, in the male, the three pairs of precloacal papillae. These specimens also ressemble, despite their longer buccal capsule, *M. dessetae*, *M. algardneri* and *M. barbarae*, which have a medium-sized body, short oesophagus and thick tail in females, and four pairs of precloacal papillae. However, *M. dessetae* has the postcloacal papilla pairs 5 and 6 in tandem but more distant from each other, a longer *area rugosa* with shorter, less widely spaced ridges (7,800, 1.5 and 6 respectively, *vs* 4,500, 2-3 and 10-14), a longer ovijector (5,200 *vs* 3,500) and a longer left spicule (260-270 *vs* 214). *M. algardneri* n. sp has a shorter *area rugosa* (2,300), a longer left spicule with a relatively short handle and long filament (270-287 and handle/blade ratio 0.88, *vs* 214 and 1.43), and no cuticular bosses on the female tail. *M. barbarae* n. sp. has a slightly concave head, a less elongated cephalic shield (cephalic ratio 1.67-2.0 *vs* 2.0-2.7), a female tail with conical and parallel lappets, a long left spicule (295), a longer *area rugosa* with longer and more widely spaced ridges (6,500, 3.5-4 and 17-18, respectively) and no cuticular bosses in the posterior part of the female body.

***Molinema nattereri* n. sp.** (Figures 8, 9)
(= *Filaria diacantha* Molin, 1858 *pro parte*)

Type-host: *Echimys* ? *didelphoides* Desmarest (I. Geoffroy) ("*Loncheres rufa* mas, Octobri") (Echimyidae).
Site: Abdominal cavity ("in cavo abdom.").

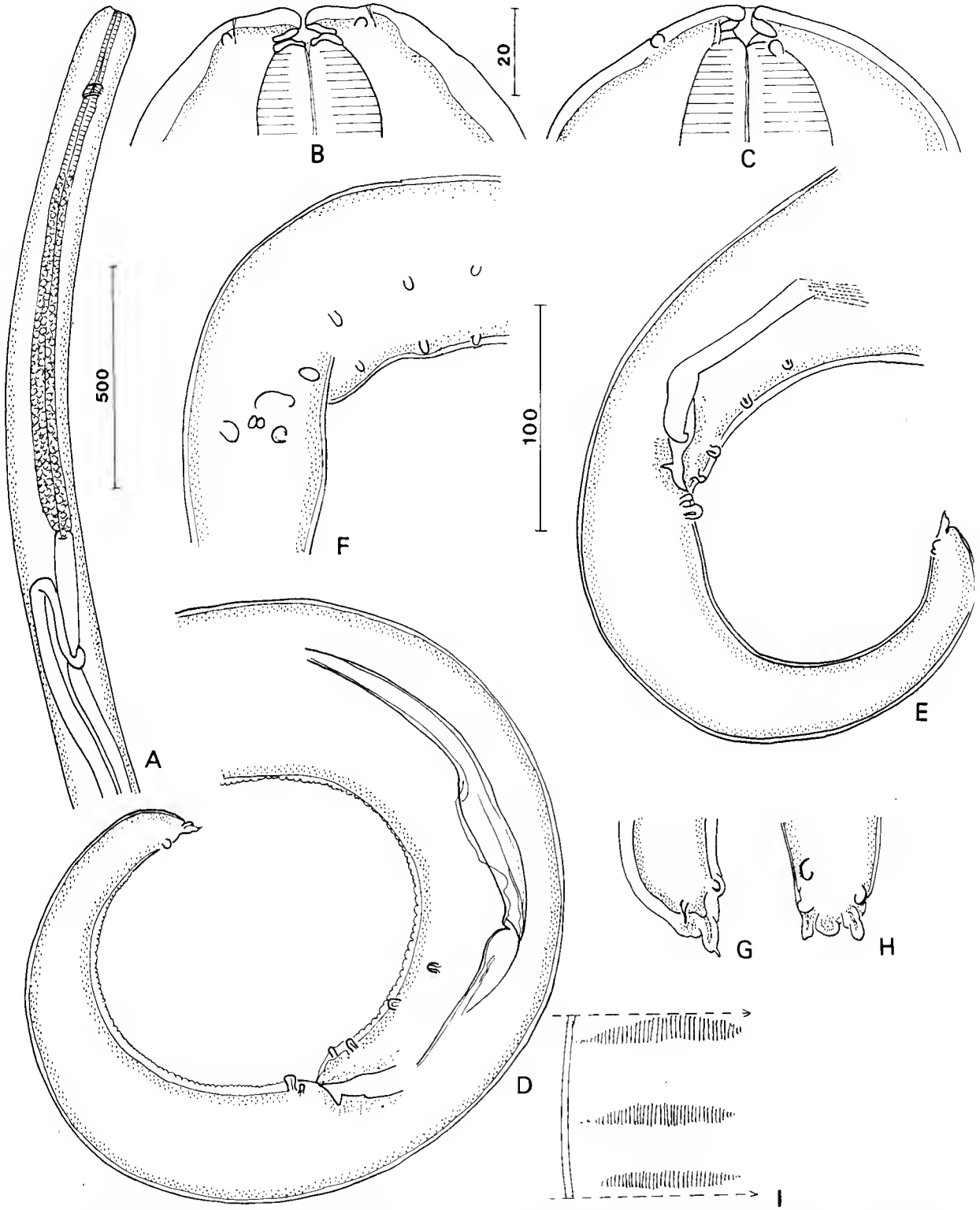

Figure 8. Molinema nattareri n. sp., male: A. Anterior region, lateral view; B. Head, ventral view; C. Head, lateral view; D. Caudal region, holotype, left lateral view; E. *Idem*, right lateral view; F. Cloacal region, paratype, ventral view; G. Caudal extremity, holotype, right lateral view; H. Caudal extremity, paratype, ventral view; I. *Area rugosa*, at mid-length. *Scale-bars*: A, 500 μm; D,E,F, 100 μm; others, 20 μm.

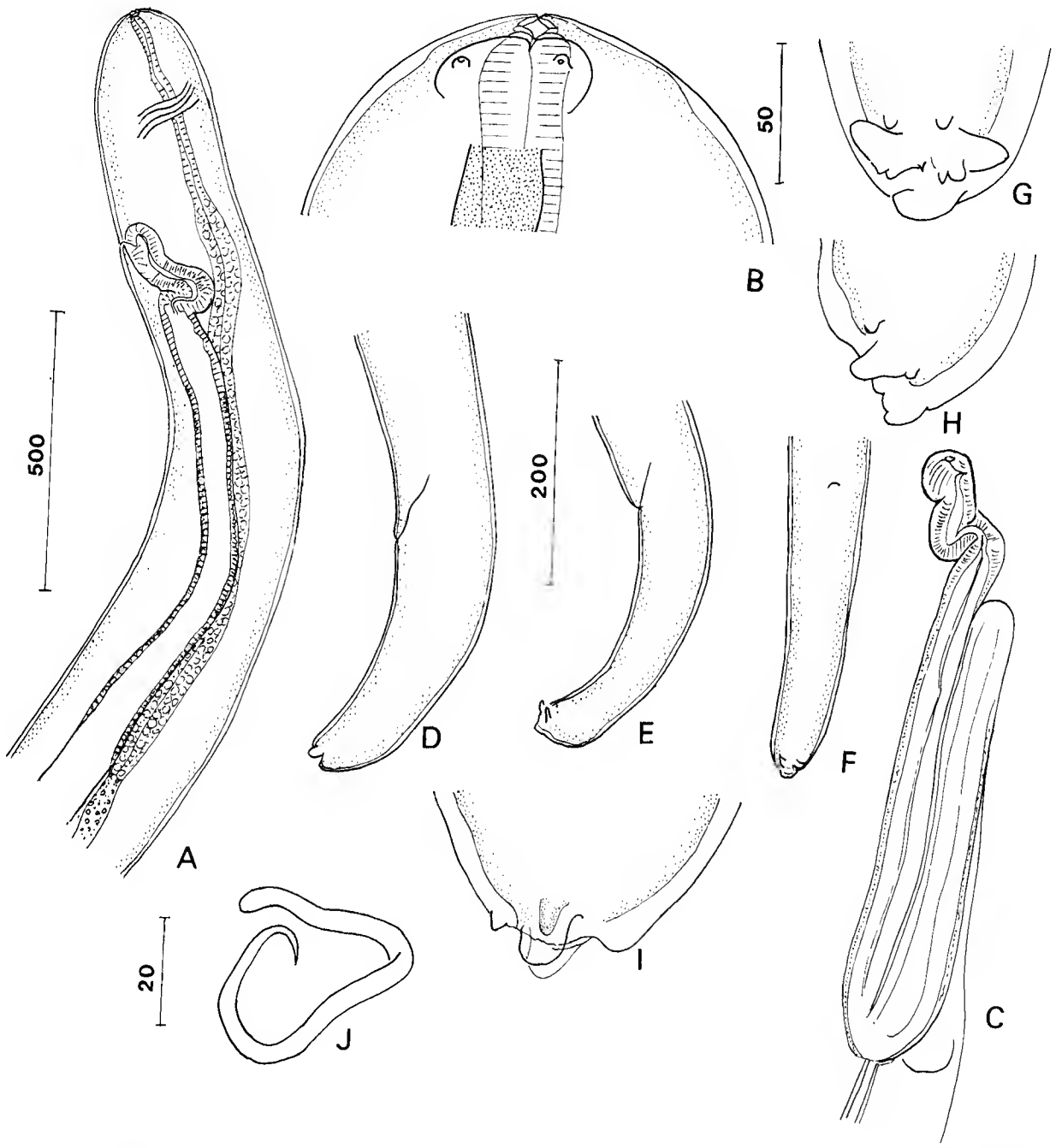

Figure 9. Molinema nattereri n. sp., female: A. Anterior region, lateral view; B. Head, lateral view; C. Ovijector; D. Tail, lateral view, paratype 1; E. *Idem*, paratype 2; F. *Idem*, ventral view, paratype 2; G. Caudal extremity paratype 2, ventral view; H. Idem, lateral view; I. Caudal extremity paratype 1, lateral view; J. Microfilaria. *Scale-bars*: A,C, 500 μm; B, 50 μm; D,E,F, 200 μm; others, 20 μm.

Type-locality: Matto Grosso ("Mato grosso")
Type-material: Holotype male, allotype (anterior part of female) and paratypes: 1 male and 1 male anterior part, 2 posterior parts of females. NMW No. 6347.
Etymology: Named for Johann Natterer, who collected these and many other hosts and parasites in Brazil during the 19th Century.

Description

General. Head flat in median view. Cephalic shield slightly expanded laterally. Buccal capsule with 2 short segments, weakly cuticularised. Oesophagus divided; glandular part slightly thicker than muscular part. Tail with conspicuous terminal tubercle in both sexes, or tail of female truncated and with median points.

Male (holotype and one paratype). Length 33.4 and 32.6 mm. Maximum width 170 and 185 at mid-body; width 120 at nerve-ring, 167 at oesophago- intestinal junction. Distance between cephalic papillae in median view 37, in lateral view 26; cephalic ratio 1.42. Buccal capsule 9 high and 16 wide. Oesophagus 1,380 and 1,530 long by 51 wide; muscular portion 380 and 420, and glandular portion 880 and 1,090. Nerve-ring 230 and 260 from anterior end. Tail 280 and 345 long; width at cloaca 55 and 61; tail ratio 5.1 and 5.6; lappets parallel 10 and 9 long. One median precloacal papilla; 3 pairs of precloacal papillae; postcloacal pairs 5 and 6 almost in transverse line; papillae of pair 5 close together; pair 6 larger; one pair of subterminal papillae anterior to lappets. *Area rugosa* 4,000 and 3,400 long; transverse ridges 6-10 high; distance between ridges 20. Cloacal wall heavily cuticularised but spicules slightly cuticularised in holotype, not identified in paratype; left spicule 260 long, with handle 90; right spicule 112 long and without heel. Spicule-ratio 2.32.

Female (2 anterior fragments, including holotype, and 2 posterior fragments). Length of anterior parts 34 and 12 mm, and posterior parts 15 and 5.5 mm. Maximum width 380 and 360 at mid-body; width at nerve-ring 223, 233 at vulva, 311 at oesophago-intestinal junction. Distance between cephalic papillae in median view 40 (allotype), in lateral view 37 (paratype). Buccal capsule 10 and 6 high and 17 and 14 wide. Oesophagus 1,480 and 1,150 long by 51 wide; muscular portion 360 and 350, and glandular portion 1,120 and 900. Nerve-ring 180 and 185 from anterior end. Vulva oesophageal, 400 and 450 from anterior end; vagina 200 and 180 long and 70 and 80 wide; unpaired ovijector 2800 long. Tail slim, bent ventrally, 270 and 250 long; width at the anus 71 and 88; tail ratio 3.8 and 2.8. Cuticle without tiny bosses. Lappets 18 long and divergent, 10 long and parallel.

Microfilaria (young coiled specimen): length 115, width 3.3.

Comments

The spicules are either very poorly sclerotised or, in the paratype, not discernable. In contrast, the dorsal wall of the cloaca is very sclerotised. As the material is well preserved, either this is a particular character of this species or, more probably, the males had moulted recently. Microfilariae in the female worms are also not fully developed. Therefore, comparison with the other species must take into account their juvenile condition.

These specimens cannot belong to *M. diacantha*. Firstly, the oesophagus in both sexes is too short: 1,150-1,530, instead of 4,200-5,980 (Freitas, 1964). Growth of this organ during the adult stage cannot explain such a difference as shown in the published data on the Onchocercidae (see Schacher, 1962; Ash & Schacher, 1971; Eberhard & Orihel, 1981, Bartlett, 1984; Bain et al., 1998) and according to our personnal observations on four species, *Litomosoides sigmodontis* Chandler, 1931, *Acanthocheilonema viteae* (Krepkogorskaya, 1933), *Molinema dessetae* and *Monanema martini* Bain, Petit & Bartlett, 1986. In all cases, the oesophageal length is no more than doubled, whereas the length of the body increases two- to thirteen-fold according to the species. Several other characters distinguish the studied material from *M. diacantha:* the female's body tends to be too wide (360-380 μm, as in *M. diacantha* but which is, however, twice as long), the ovijector is longer (2,800 *vs* 1,660-2,240, in Freitas, 1964), the microfilariae, which are immature and thus probably not as slender as they would have become later, are thinner (3.3 *vs* 8), and, finally, the fouth pair of caudal papillae, which are reduced in *M. diacantha*, have disappeared in the studied specimens.

This last character brings these specimens closer to *M. bifida, M. proechimyis* and *M. raposoensis*. However, *M. bifida* and *M. proechimyis* are distinguished by the longer and differently shaped buccal capsule (such a sclerotised organ hardly changes during adult life). *M. raposoensis* has a slim tail like our specimens,

but differs in that the papillae of pair 5 are not contiguous in the median line, the precloacal papillae are closer to the cloaca, the anterior region of the female body is only half as wide, and the cephalic shield is broader.

General discussion on the history of the genus *Molinema*

Twelve species are presently known in the genus *Molinema*. They are host- specific, except for one species, *M. proechimyis*, which is parasitic in two genera of the Echimyidae, *Proechimys* and *Echimys*, in Trinidad (Esslinger, 1974; Everard et al., 1974); this could be linked to the particular conditions existing on an island.

Molinema is considered to be a small branch of the more ancient and cosmopolitan *Dipetalonema*-line (Chabaud & Bain, 1976) and is characterised by the persistence of several primitive characters, such as deirids, the divided oesophagus with a triradiate lumen, the well-developed caudal lappets, and the arrangement of the cloacal papillae close to the ancestral spirurid type (several precloacal pairs in two rows, pairs 5 and 6 posterior to the cloacal aperture, and a terminal group of papillae).

The history of *Molinema* appears almost exclusively linked to two Neotropical rodent families, the Erethizontidae and the Echimyidae. These represent only a small part of the present-day Caviomorpha *sensu* Wood, 1955 (South American Hystrichognathi) and, according to a recent review (Hartenberger, 1998), they belong respectively to the infra-orders Erethizontida (one family) and Caviida (the remaining nine families).

Molinema might be derived from Palaeoendemic forms of the *Dipetalonema*-line (Chabaud & Bain, 1976) and related species. A parasite of South American marsupials, *Skrjabinofilaria skrjabini* Travassos, 1925, develops in mosquitoes, like *Molinema* spp., the third stage larva has a mouth opening flattened laterally, as in *M. dessetae*, and the *area rugosa* of the adult male begins on the tail itself and not anterior to it.

Or *Molinema* might be derived from Ethiopian forms, such as *Acanthocheilonema* Cobbold, 1870 (Bain et al., 1982). This supposes that their hosts, the Ethiopian Hystrichognathi, migrated into South America. Caviomorphs cannot be traced back further than the early Oligocene in South America (Vucetich et al., 1999) and their origin remains debatable (Hoffstetter & Lavocat, 1970; Hartenberger, 1998). However, such an hypothesis is supported by two other groups of nematodes, the trichostrongylid heligmosomes (Durette-Desset, 1971) and some oxyurids (Quentin, 1973; Hugot, 1982): in these examples, there are great similarities between the parasites of African and South American porcupines.

The present data on *Molinema* do not allow resolution of the question of the origin of this genus. However, the Erethizonthidae seem to harbour more primitive *Molinema* species. Indeed these filarial species, *M. diacantha* and *M. arbuta*, have a long oesophagus (> 2 mm) and a complete set of precloacal papillae. These characters are, however, associated with evolved characters; they are differently combined in the two species and this suggests wider radiation of this line in the past. *M. diacantha* has an evolved head (concave with a high cephalic ratio) and, in contrast, a long buccal capsule and, in the male, caudal alae and large pedunculate precloacal papillae. *M. arbuta* is characterised by the primitive state of the head (flat, with lateral edges not bulging) but it has an advanced reduction of the buccal capsule.

The nine *Molinema* species parasitic in the Echimyidae do not have such a well-developed oesophagus as the two species from the Erethizontidae. However, these two groups of *Molinema* species do not diverge significantly, as the biology and morphology of the infective larva are similar (Bain & Chabaud, 1986). The precloacal papillae are reduced to three pairs in some species, but none has a minute buccal capsule. Seven species are parasites of the well-diversified genus *Proechimys*, which is geographically widespread, abundant and readily trapped; they can be distinguished from each other by the different combinations of the characters of the head and capsule, pre- and post-cloacal papillae, spicules, *area rugosa*, ovijector, and shape and cuticular ornamentation of the female's tail, caudal lappets' terminal tubercle and microfilariae. The species with the most evolved head, either very much expanded laterally or concave, are located outside the Amazonas basin; these are *M. raposoensis* in the Pacific area of Colombia and *M. proechimyis* in Trinidad. *M. bifida*, from a member of the Dactylomyinae (*Kannabateomys*) in Brazil, has conserved a head with a small cephalic ratio and a large buccal capsule, but the concave head and the precloacal papillae, reduced to three pairs, are evolved characters. *M. travassosi*, parasitic in *Myocastor*, does not have any special distinguishing features, except the great size of the body and the left spicule; this

agrees with the modern classification of this rodent, which is no longer isolated in its own particular family (Vucetich et al., 1999).

The last species, *M. sprenti*, is a parasite of the Castoridae. It has a primitive oesophagus and flat head, but a minute buccal capsule, and is close to *M. arbuta*. In addition, these two species have long microfilariae (about 300-400 μm). Both are found in the Nearctic region. The parasite of the Castoridae, with a more extended cephalic shield (ratio 1.9 rather than 1.4) and an unusually long and spirally coiled tail in the female, is thus thought to have been derived from the species parasitising the Erethizontidae by "capture" (*sensu* Chabaud, 1982). It was contemporary with the migration of some Neotropical Erethizontidae to North America, which occurred after the two American continents were united, about 3 mya (Pleistocene).

As often observed in filarial parasites, which are nematodes transmitted by haematophagous vectors, the "capture" of new host groups, favoured by an expanding and new geographical distribution of an original host group, is an important factor in evolution. This probably occurred with the Castoridae in North America. However, the recent diversification of the Muridae (Sigmodontinae) in South America has not induced any new diversification of the genus *Molinema*. These modern rodents, which are often trapped in the same localities as infected echimyids, have never been found infected with species of *Molinema*; they are, however, often infected with representatives of the genus *Litomosoides* Chandler, 1931 (Esslinger, 1963, 1973; Notarnicola et al., 2000).

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